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ESTIMATING ABUNDANCE FROM REPEATED PRESENCE–ABSENCE DATA OR POINT COUNTS

J. Andrew Royle[1,3] and James D. Nichols[2]

[1]*Division of Migratory Bird Management, U.S. Fish and Wildlife Service, 11510 American Holly Drive, Laurel, Maryland 20708 USA*
[2]*U.S. Geological Survey, Patuxent Wildlife Research Center, 11510 American Holly Drive, Laurel, Maryland 20708 USA*

Abstract. We describe an approach for estimating occupancy rate or the proportion of area occupied when heterogeneity in detection probability exists as a result of variation in abundance of the organism under study. The key feature of such problems, which we exploit, is that variation in abundance induces variation in detection probability. Thus, heterogeneity in abundance can be modeled as heterogeneity in detection probability. Moreover, this linkage between heterogeneity in abundance and heterogeneity in detection probability allows one to exploit a heterogeneous detection probability model to estimate the underlying distribution of abundances. Therefore, our method allows estimation of abundance from repeated observations of the presence or absence of animals without having to uniquely mark individuals in the population.

Key words: abundance estimation; Breeding Bird Survey; detection probability; mixture models; occupancy rate; patch occupancy models; point counts; presence–absence data.

Introduction

Estimation of abundance for animal populations involves two basic issues (e.g., see Thompson 1992, Lancia et al. 1994, Skalski 1994, Thompson et al. 1998, Yoccoz et al. 2001). First, the investigator is sometimes interested in areas that are sufficiently large that ground surveys cannot be conducted over the entire area of interest. In such situations, investigators must select a sample of locations to survey, and the selection must be conducted in a manner that permits inference about the entire area of interest, and thus about the locations not sampled. This is a standard problem in spatial sampling; statistical texts such as Cochran (1977) and Thompson (1992) present sampling designs and associated estimators to permit such inference. The second problem in animal abundance estimation involves detectability, or the idea that animal survey methods seldom detect all animals present in any surveyed area or sample unit. Instead, animal survey methods involve collection of some sort of count statistic, and the investigator then must develop an estimator for the probability that an animal present in the area of interest appears in the count statistic. This probability also can be viewed as the expected proportion of the animals present that is actually detected. The variety of methods presented in texts (e.g., Seber 1982, Buckland et al. 2001, Williams et al. 2002) and reviews (Lancia et al. 1994) of animal abundance estimation provide different methods of estimating detection probabilities for specific kinds of count statistics.

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[3] E-mail: andy_royle@fws.gov

Methods for estimating detection probabilities, and thus abundance, on sample units can be expensive in both time and effort. For example, capture–recapture methods require repeated efforts to capture or observe animals (Otis et al. 1978, Pollock et al. 1990). Even observation-based methods such as distance sampling (Buckland et al. 2001) and multiple observers (Cook and Jacobson 1979, Nichols et al. 2000) are viewed by some as too consumptive of time and effort.

One potential approach to reducing effort in large-scale monitoring programs involves a shift of interest from numbers of animals to numbers of sample units occupied by animals. Methods implementing this general approach are based on presence–absence (more properly, detection–nondetection) data obtained on sampling units. Such methods have been developed independently several times (Geissler and Fuller 1987, Azuma et al. 1990, Bayley and Peterson 2001, MacKenzie et al. 2002, Nichols and Karanth 2002) and appear to be useful for a variety of different monitoring programs (e.g., patch occupancy by spotted owls in western North America, area occupancy by tigers in India, wetland occupancy by anurans throughout North America). In addition to providing a reduced-effort approach to large-scale monitoring, surveys directed at occupancy are very useful for metapopulation studies (e.g., see Hanski and Gilpin 1997). The proportion of patches occupied is viewed as a state variable in various metapopulation models (e.g., Levins 1969, 1970, Hanski 1992, 1994, 1997, Lande 1987, 1988). Many metapopulation studies also focus on so-called ''incidence functions'' (e.g., see Diamond 1975, Hanski 1992) in which the probability of occurrence of a species in a patch is expressed as a function of patch characteristics such as area and habitat.

Estimation approaches developed for occupancy surveys incorporate detection probability directly into the estimation process (see MacKenzie et al. 2002) and thus deal appropriately with this fundamental component of animal abundance estimation. It is not necessary to count the numbers of organisms observed on sample units, and occupancy surveys are thus relatively easy and efficient to conduct. As with traditional capture–recapture studies, the possibility that heterogeneity exists in detection probability is an important modeling consideration. One important source of heterogeneity, probably *the* most important source in many situations, is variation in animal abundance, N, among sites. Variable N induces heterogeneity in site-specific detection probabilities. Thus, failure to accommodate heterogeneity in detection probability is a de facto assumption of constant abundance among sites.

To illustrate this linkage between abundance and heterogeneous detection probabilities, suppose that the ith sample unit is occupied by N_i animals, that all animals in a sample unit have identical detection probabilities, and that detection of an individual animal in a sample unit is independent of detection of other animals in that unit. In this situation, the conditional (on N_i) probability of detecting occupancy on a sample unit, say p_i, can be written as

$$p_i = 1 - (1 - r)^{N_i} \tag{1}$$

where r is a binomial sampling probability that a particular individual is detected. Detection probability at the level of the sample unit p_i is estimated via repeat visits by investigators to the sample units (e.g., MacKenzie et al. 2002). That approach requires that a group of sample units either have the same p_i or else have p_i that vary in accordance with measurable covariates, and therefore it is inappropriate when p_i varies as a result of variation in N_i.

This relationship suggests that if one is able to adequately characterize the distribution of detection probabilities, then the distribution of abundances can be deduced from Eq. 1. Because one of the main perceived limitations of occupancy surveys is their inability to generate information about absolute abundance, such a framework may greatly expand the utility of occupancy surveys in many settings.

In this paper, we provide a method for: (1) dealing with heterogeneity in detection probabilities caused by variation in animal abundance, and (2) using this heterogeneity to extract information about abundance from occupancy surveys. Our approach is to acknowledge that heterogeneity in N_i induces heterogeneity in p_i according to Eq. 1. When properly specified to acknowledge this, a mixture distribution for p_i permits estimation of the distribution of N_i. From this estimated distribution, the best estimate of N_i, given the data at a particular site, can be computed. The estimated distribution of abundances across sites, $\{\hat{N}_i;\ i = 1, 2, \ldots,\}$, is useful in certain kinds of metapopulation modeling (see *Discussion*). In addition, these estimates of N_i are useful for estimating two important quantities. First, the estimates can be summed over all sites to estimate overall abundance on the sample units or average abundance per sampled unit. Second, the estimated fraction of occupied sites ($N_i > 0$) estimates occupancy probability in a manner that deals directly with the heterogeneity associated with the variation in unit-specific abundances.

Occupancy Surveys

Occupancy surveys entail repeat visits to R sample units $i = 1, 2, \ldots, R$ (we refer to these as ''sites''). At each visit, an effort is made to detect the species of interest, producing a detection history of whether or not the species was detected at each of the visits to the site. The observed presence–absence at each visit is a binary random variable defined as follows:

$$w_{it} = \begin{cases} 1 & \text{if detected at site } i \text{ in sample } t \\ 0 & \text{if not detected.} \end{cases}$$

We note that the key element of this problem is that observed nondetection is ambiguous, in the sense that there may be nondetection at sites that are, in fact, occupied (sampling zeros) and nondetection as a result of a site being unoccupied (fixed zeros). The important estimation problem is the separation of these two types of zeros by parameterizing a model that allows estimation of both detection probability and occupancy rate.

The likelihood of the data is constructed by acknowledging that the site-specific detection frequencies, $w_{i.} = \sum_t w_{it}$, are a mixture of two processes. One process is the usual binomial likelihood found in many capture–recapture problems. This model is *conditional* on animals being present at site i (i.e., occupancy) and available for counting. Sampling zeros may result from this binomial sampling model. We assume that each site has probability ψ of being occupied. Thus, the second process is that $w_{i.}$ has a point mass at 0 with probability $1 - \psi$. That is, if animals are not present, then $\Pr(w_{i.} = 0) = 1$. This component model generates the fixed zeros.

From these considerations, the marginal likelihood of the data may be constructed. This may be found in MacKenzie et al. (2002), for example. The simple closed-population, constant-p version with T sample periods is

$$L(\mathbf{w}) = \left\{ \prod_{w_{i.}>0} \binom{T}{w_{i.}} p^{w_{i.}} (1 - p)^{(T - w_{i.})} \psi \right\} \times \left\{ \prod_{w_{i.}=0} [\psi(1 - p)^T + (1 - \psi)] \right\} \tag{2}$$

where $w_{i.}$ is the number of times that detection occurred at site i, and p is the conditional (on occupancy) probability of detection, i.e., analogous to the usual capture–recapture detection probability parameter. It is a simple matter to numerically maximize this likelihood in order to obtain estimates of p and ψ.

This basic occupancy model is often referred to as a zero-inflated binomial model (e.g., Hall 2000) in other applications. Zero-inflation models are commonly used for modeling count data that contain excessive zeros, including Poisson and negative binomial models. Extension of this concept to any distribution is, in principle, straightforward.

As specified here, data consist of detection or nondetection. In practice, counts or some other ordinal measures of abundance may be observed. Such data can be reduced to a binary (presence–absence) response and model 2 can be applied. Also, possibilities exist for making direct use of data other than detection–nondetection, such as counts, although methods for handling more general problems must be developed. We address this further in the *Discussion*.

The occupancy survey model as a finite mixture on p

The argument producing the likelihood in Eq. 2 is that there are two classes of sites, those that are occupied and those that are not. Then, conditional on occupancy, animals are detected with probability p.

An alternative way to develop this model is to assume that each site has its own detection probability, say p_i, and that there are two possible values of p_i. First, a constant, nonzero p, say $p_i = p_1$, which occurs with probability ψ. Sampling from such a site will yield $w_{i.}$ according to the usual binomial (T, p_1) sampling model. Second, define ''unoccupied'' sites to have zero capture probability, i.e., $p_i = 0$, so that $\Pr(w_{i.} = 0) = 1$, which occurs with probability $1 - \psi$. In this case, $w_{i.}$ is sampled from a binomial $p = 0$ distribution, which, of course, always will yield $w_{i.} = 0$. This formulation as a mixture of binomial random variables with different values of p, and mixing proportion ψ, is equivalent to the earlier construction as a mixture of a binomial random variable conditional on occupancy, and a point mass at 0. That is, both yield the likelihood of Eq. 2.

When viewed as a mixture on detection probability, this type of problem is similar to the finite-mixture models considered by Norris and Pollock (1996) for modeling heterogeneity in capture probabilities among animals in a traditional N estimation framework, with the exception that the finite mixture in Norris and Pollock (1996) is specified on the *conditional* capture probabilities, which are assumed to be nonzero for all animals in the population. Here, we have simply marginalized the likelihood over two capture probability states, one of which is zero, with the implicit understanding that sites with $p_i = 0$ are unoccupied sites, i.e., that animals cannot be detected at those sites. That is, the detection probability under this alternative development is a *marginal* detection probability.

Modeling Heterogeneity in p With Finite Mixtures

We suppose that the number of animals available for detection, N_i, varies among sites. As is customary in other capture–recapture type problems, we assume that the events during which individual animals at a site are detected are independent of one another. Let y_i be the number of animals observed. Then, the probability of detecting at least 1 animal, *given* that animals are present, is equal to 1 minus the probability of *not* detecting all N_i animals at the site:

$$\begin{aligned} p_i &= \Pr(y_i > 0 \mid N_i) = 1 - \Pr(y_i = 0 \mid N_i) \\ &= 1 - (1 - r)^{N_i}. \end{aligned}$$

We see that variation in N_i is manifest as heterogeneity in capture probability. We note that, in many problems where the focus is on the proportion of the area occupied, only the event that $y_i > 0$ (or $y_i = 0$) is observed (see *Discussion*), but for the development of the model, it is useful to think in terms of the site-specific count, y_i.

Consequently, unless one believes that abundance is constant among sites, it is important to accommodate variation in capture probability among sites that is a result of variation in N_i. This relationship further suggests that modeling heterogeneity in p_i will allow characterization of the distribution of N_i, because distinct values of p_i result only from variation in N_i.

In the following development, we suppose that detection probability varies by sample location only according to the number of animals available to be detected, $p_i = 1 - (1 - r)^{N_i}$. One could impose additional model structure on r, which we discuss shortly. We emphasize here that p_i is defined conditional on N_i, which may be zero. This is in contrast to the traditional development presented in *Occupancy Surveys*, where detection probability is defined conditional on $N_i > 0$. We discuss this further in *Conditional and unconditional detection probability*. The particular case where $N_i = 0$ is important because in this case we have $p_i = 0$. That is, if a site is unoccupied, then the probability of detection at that site is 0, which is the alternative development of the occupancy model alluded to in *Occupancy Surveys*, based on a finite mixture on marginal detection probability.

For site i, let $w_{i.}$ be the number of detections observed in T repeated samples. Then, $w_{i.}$ is a binomial random variable with likelihood

$$L(w_{i.}) = \binom{T}{w_{i.}} p_i^{w_{i.}} (1 - p_i)^{T - w_{i.}}.$$

It is difficult to obtain reasonable estimates of each p_i for realistic values of T. Moreover, it is even less clear how to obtain an estimate of abundance from this likelihood. However, we can exploit the relation between p_i and abundance to make progress in this regard.

We now suppose that abundance is a random variable with some probability distribution, say $\Pr(N = k) = f(N = k) = f_k$. Thus, the site-specific abundances, N_i; $i = 1, 2, \ldots$, are viewed as realizations of the random variable N having probability distribution $f(N)$. Because the random variable N is discrete, the density of site-specific detection probabilities, p_i, has support on the values $p_k = 1 - (1 - r)^k$ for $k = 0, 1, \ldots$. Moreover, because of the relationship between p_k and N, $\{f_k\}$ is also the density for p_i; i.e., $\Pr(p_i = p_k) = f_k$.

If the particular values of N_i were known, then one could simply estimate r from the likelihood conditional on N. However, site-specific abundances are unknown. A standard trick in similar problems involving random effects or nuisance parameters is to estimate parameters of the marginal likelihood of $w_{i.}$, which is the following mixture:

$$L(w_{i.}) = \sum_{k=0}^{\infty} \binom{T}{w_{i.}} p_k^{w_{i.}} (1 - p_k)^{T - w_{i.}} f_k. \tag{3}$$

The goal is to estimate r, the animal-specific detection probability relating the mass points, and their masses f_k. Without further assumptions, this infinite-dimensional estimation problem cannot be solved. One reasonable assumption is to impose a parametric form on f_k (we discuss specifics in the section *Estimation of the Mixing Distribution and Abundance*). Although this does not require limiting the number of support points, one would likely do so for numerical analysis of the likelihood. In this case, with K support points, we have

$$L(w_{i.}) = \sum_{k=0}^{K} \binom{T}{w_{i.}} p_k^{w_{i.}} (1 - p_k)^{T - w_{i.}} f_k. \tag{4}$$

This has the appearance of the finite-mixture model proposed by Norris and Pollock (1996). In their statement of the problem, K would be limited by the number of sampling occasions because the number of parameters to be estimated increases with K. With a parametric form imposed on f_k, this is not necessary, except in the numerical analysis of the likelihood.

For independent data from R sites, $\mathbf{w} = (w_{1.}, w_{2.}, \ldots, w_{R.})$ the likelihood is the product of R versions of Eq. 4:

$$L(\mathbf{w}) = \prod_{i=1}^{R} \left\{ \sum_{k=0}^{K} \binom{T}{w_{i.}} p_k^{w_{i.}} (1 - p_k)^{T - w_{i.}} f_k \right\}. \tag{5}$$

The fact that the masses of the support points in this finite mixture correspond to *abundance* classes is crucial to being able to estimate abundance from presence–absence data. Application of finite mixtures on detection probability to the problem of occupancy surveys generates an estimated mixing distribution that is, by construction, an estimate of the distribution of animal abundance among sites. Estimation of this model will be discussed shortly, including selection of the masses.

Relationship to model ''M_h''

This model is analogous to the finite-mixture distributions used by, for example, Norris and Pollock (1996) and Pledger (2000) for the modeling of heterogeneity in animal-specific capture probabilities (so-called ''Model M_h''), in the sense that the model is of heterogeneity in detection probability among sample units. In traditional applications, sample ''units'' are individual animals (being captured and recaptured), whereas in occupancy applications, ''units'' are spatial units wherein animals are repeatedly detected or not detected. Some discussion of this issue also is given in MacKenzie et al. (2002).

There are several important practical differences between the model described by Eq. 5 and traditional applications of model M_h that merit further discussion. First, in the present problem, the *discrete* support of p_i is a direct consequence of the discrete support of the random variable N. In traditional applications, the discrete support of p_i is merely a convenient modeling decision. Second, the support points are *known* except for the unknown parameter r, and are specified by the expression $p_k = 1 - (1 - r)^k$ for $k = 1, 2, \ldots, K$, the support of the distribution of N_i. The only unknowns are the densities of the support points and the animal-specific capture probability, r. In general problems involving heterogeneity, continuous mixtures may be more appropriate, e.g., the beta mixture (Burnham and Overton 1978, Dorazio and Royle 2002). However, discrete mixtures are especially relevant for this particular problem because of the nature of the heterogeneity, as arising from variation in N (which is discrete). Third, in traditional applications of finite mixtures, the finite mixture is imposed on the *conditional* (on occurrence) capture probability. In the present development, the event that a site is *not* occupied is equivalent to that site having $p_i = 0$, as a result of $N_i = 0$. Thus, it is sensible to think of a portion of the population with zero capture probability, and to model this case as simply another support point for the mixing distribution of the *marginal* detection probability p_i. Then, the zero point mass ($\Pr(p_i = 0)$) is the occupancy rate parameter.

Alternative models for detection

Although the model has been presented assuming that r is constant, this is no more necessary here than it is in any other capture–recapture type of problem. For example, if r varies according to certain site or time-specific covariates, then the model could be extended to accommodate them. Natural candidates that influence detection probability are weather or sampling conditions, or simply time (i.e., r varies over the study). We provide an example of this in *Application to Avian Point Counts*.

Observation of simple presence–absence does come at some expense with regard to modeling structure on r. Because recapture information is unavailable on *individual* animals, obviously one cannot accommodate individual heterogeneity in detection probability. Of course, this is a consideration in any study design; thus, in problems in which individual heterogeneity is thought to be critical, one should conduct a capture–recapture study with unique marking of individuals. Even though individual animal heterogeneity may be important in many problems, relevant data often are not collected, which of course motivates the general interest in occupancy-type problems. Regardless, heterogeneity among spatial units as a consequence of variable abundance will generally be important unless one believes that abundance is constant among sites, which is biologically untenable in many situations, but perhaps reasonable in others (see *Discussion*).

Conditional and unconditional detection probability

Because conventional thinking in capture–recapture problems is based on the notion of a capture probability defined conditional on presence, or occupancy, it is instructive to clarify the relationship between the unconditional capture probability that forms the basis of the likelihood given by Eq. 5 and the more conventional definition.

We first consider the unconditional detection probability. This is the probability of detection, regardless of whether or not a site is occupied. Because occupancy states are indexed by abundance, this average detection probability may be expressed as the average over the unoccupied ($N = 0$) and various occupied ($N > 0$) states as

$$\bar{p} = \sum_{k=0}^{\infty} \Pr(y > 0 \,|\, N = k)\Pr(N = k). \tag{6}$$

We emphasize that $\bar{p}$ is the average probability of detecting animals on any particular sample unit that includes the $p_i = 0$ possibility, which is ''non-occurrence.'' In this sense, it differs from the detection probability parameters typically considered in animal abundance estimation problems. However, this is sensible in occupancy survey problems because of the duality between a finite mixture on occupancy state and a finite mixture on unconditional detection probability including the 0 state (i.e., *Occupancy Surveys*).

To determine the relationship between $\bar{p}$ and the more familiar *conditional detection probability*, note that Eq. 6 is the same as

$$\begin{aligned}\bar{p} = {} & \Pr(y > 0|N > 0)\Pr(N > 0)\\ & + \Pr(y > 0|N = 0)\Pr(N = 0)\end{aligned}$$

where, of course, the second term is 0. Here, $\Pr(y > 0|N > 0)$ is the *conditional* (on occupancy) detection probability, which we will denote as $\bar{p}_c$. Also, $\Pr(N > 0)$ is the occupancy rate, analogous to ψ in Eq. 2. Therefore,

$$\bar{p} = \bar{p}_c\psi$$

and hence,

$$\bar{p}_c = \frac{\bar{p}}{\psi}$$

or, using Eq. 6,

$$\bar{p}_c = \sum_{k=1}^{\infty} \Pr(y > 0 \,|\, N = k)\frac{\Pr(N = k)}{\psi}. \tag{7}$$

This *is* analogous to the usual detection probability parameter (e.g., that of MacKenzie et al. [2002]), in the sense that it is conditional on animals being present and available for detection. The difference between this expression and the traditional conditional detection probability is, of course, that $\bar{p}_c$ is a mixture of different detection probabilities that depend on N.

Similarly, one can compute the variance (or standard deviation) of the p_i's either conditional on $N_i > 0$ or not. In the simulation studies discussed in the section *Simulation Study*, we report the conditional standard deviation, say σ_c, as a measure of the induced heterogeneity in p_i resulting from variation in abundance. As with $\bar{p}_c$, σ_c will depend on the abundance distribution. This parameter may be interpreted in the same manner as that found in traditional situations involving Model M_h (e.g., Burnham and Overton 1978, Pollock and Norris 1996, Dorazio and Royle 2002). For example, larger values of σ_c imply more heterogeneous p_i's, in which case the ''constant p'' models will perform relatively poorly.

Estimation of the Mixing Distribution and Abundance

Estimation of the mixing distribution may proceed in two ways. First, we may adopt the nonparametric approach laid out in Norris and Pollock (1996) and Pledger (2000). The number of nonzero support points that may be considered in this situation is limited by T, so where the range of N_i is large, the nonparametric approach will lead to a coarse approximation to the true underlying distribution.

The second approach, and the one that we prefer, is to consider parametric forms for the masses f_k. Perhaps the most natural candidate for f is the Poisson density, $N_i \sim$ Poisson (λ), so that

$$f_k = \frac{e^{-\lambda}\lambda^k}{k!} \tag{8}$$

where λ is the Poisson intensity parameter to be estimated. This expression may be substituted into Eq. 5, along with $p_k = 1 - (1 - r)^k$, yielding a model with only two parameters, λ and r.

The Poisson model is a natural assumption for modeling abundance for two reasons. First, suppose that N_i were observable *without error*, and interest was in constructing statistical models that explain variation in the N's. The most obvious modeling approach for such data is a Poisson generalized linear model (GLM) with a log-linear model explaining variation in the mean of N. This is classical Poisson regression, analogous to linear regression for normal data. In the present context, the Poisson regression model functions as a prior distribution for the unobservable abundances. Seber (1982) provides other instances in which the Poisson assumption is useful. Second, the Poisson model for abundance arises under a random distribution of animals in space, and hence it is popular in many ecological studies involving the distribution of plants and animals.

Many other models for abundance are possible. A second model that we consider here is the negative binomial model (e.g., Lawless 1987) given by

$$\Pr(N = k) = \frac{\Gamma(k + a)}{k!\Gamma(a)}\left(\frac{(1/a)\mu}{1 + (1/a)\mu}\right)^k\left(\frac{1}{1 + (1/a)\mu}\right)^a \quad (9)$$

where a and μ are the parameters, and the mean and variance under this model are

$$E[N] = \mu$$

and

$$\text{Var}[N] = \mu + \frac{\mu^2}{a}.$$

The negative binomial model can be viewed as a mixture of Poisson distributions with means that vary according to a gamma distribution. This may be an appealing model in some instances because it allows the density of animals to vary spatially. Thus, the negative binomial model can allow for more variation in abundance than can be described by a constant mean Poisson model (extra-Poisson variation in N, or overdispersion).

The benefit of using a parametric density for abundance is a great reduction in the number of parameters to be estimated (i.e., to one parameter describing the support points and one describing their masses) compared with the nonparametric finite-mixture models of Norris and Pollock (1996), wherein the number of parameters increases with the number of support points defining the mixture. Additionally, with a parametric mixing distribution, the support of N need not be artificially restricted so as to ensure identifiability of model parameters.

Estimation by maximum likelihood proceeds as described in Pledger (2000), except for f_k being constrained according to Eqs. 8 or 9, and with support points specified by $p_k = 1 - (1 - r)^k$. Thus, the two parameters to be estimated are the animal-specific detection probability, r, and λ, the mean of this Poisson distribution on N. Using these estimates, we may estimate $\{f_0, f_1, \ldots, f_K\}$, the set of probabilities $\Pr(N = k)$, and the corresponding support points, p_k.

Estimating occupancy

Under a parametric model such as the Poisson, $\psi = 1 - f_0$ is a derived parameter (i.e., implied by λ), and so an estimator of ψ under the Poisson model, for example, is $1 - \Pr(N = 0; \hat{\lambda})$:

$$\psi = 1 - e^{\hat{\lambda}}.$$

Estimating abundance

We may compute $\Pr(N_i = k|w_{i.})$ given the total number of detections at each site, $w_{i.}$, using Bayes theorem:

$$\Pr(N_i = k \mid w_{i.}) = \frac{\Pr(w_{i.} \mid N_i = k)\Pr(N_i = k)}{\sum_{k=1}^{K} \Pr(w_{i.} \mid N_i = k)\Pr(N_i = k)}. \quad (10)$$

Note that $\Pr(w_{i.}|N_i = k)$ are simply binomial probabilities, and $f_k = \Pr(N_i = k)$, for which we may use the estimates, $\hat{f}_k$.

The posterior masses from Eq. 10 may be computed for each value of k. One could use as an estimate of N_i that value of k that produces the highest posterior probability (i.e., the posterior mode). Alternatively, we prefer using the posterior mean:

$$E[N_i \mid w_{i.}] = \sum_{k=1}^{K} k \times \Pr(N_i = k \mid w_{i.})$$

which will not usually be an integer. Other characteristics of the posterior of N_i (e.g., the variance, percentiles, etc. . . .) may be computed using the posterior probabilities in Eq. 10.

In many problems, one would expect abundance to be small at a local scale; consequently, estimates for N_i's will be very poor. However, this framework may produce very good estimates of the *total* or *average* number of individuals present at the collection of sites sampled. Of course, $\hat{\lambda}$ *is* an estimate of the average, and, where R sites are sampled, $R\hat{\lambda}$ is an estimate of the total abundance on the R sample units. When sampling units are inherently discrete, such as wetland basins in amphibian surveys, or in waterfowl breeding pair counts or brood counts, then the total abundance in a region of interest may be estimated directly by area expansion. Otherwise, when the effective area of a sampling unit is known, then an estimate of total abundance may be obtained by a simple area expansion.

Application to Avian Point Counts

Avian point counts are widely used to investigate problems in avian biology and ecology. Because it is sometimes difficult to determine the number of unique individuals observed, the use of presence–absence data for the analysis of occupancy and other questions is appealing. Here, we demonstrate the application of our method for estimating abundance from simple presence–absence data based on avian point counts. The data were collected on a North American Breeding Bird Survey (BBS) route in New Hampshire in 1991. The data were collected at 50 points (''stops'') over a period of 30 days during the BBS sampling interval. The 50 points were sampled 11 times each by the same observer. For general background on the BBS, see Robbins et al. (1986). For further description of the data used here, see Link et al. (1994). We consider five species for analysis: Hermit Thrush (*Catharus guttatus*), Wood Thrush (*Hylocichla mustelina*), Gray Catbird (*Dumetella carolinensis*), Ovenbird (*Seiurus aurocapillus*), and American Redstart (*Setophaga ruticilla*).

We make use of the Poisson assumption on abundance at the stop-level, as described in the previous section. We believe that the assumption that N_i is constant over the time period in question is reasonable, on the grounds that birds have established breeding territories at that time. No stop-specific covariates are available to allow for the modeling of variation in stop-level abundance. In general, such information could be modeled in the Poisson mean, as in traditional generalized linear models. An important aspect of these data is that breeding activity may vary over the period in question, which suggests that the detection probability *may* vary over the course of the study as a result of variation in nesting or calling activity. Because of this, we considered several alternative models for detection probability, based on a logistic model for detection probability according to

$$\text{logit}(r_{\text{day}}) = \beta_0 + \beta_1\text{day} + \beta_2\text{day}^2. \tag{11}$$

Here, the variable ''day'' indexes the day on which the sample was conducted from the beginning of the study. The three models considered were those submodels containing only β_0 (Model 1 [M1], constant detection probability), β_0 and β_1 (Model 2 [M2], linear change in detection probability) and all three parameters (Model 3 [M3]), allowing for quadratic change in detection. For example, quadratic change might involve an increase in detectability followed by a decrease, or vice versa.

In addition to these models allowing for temporal variation in detection probability and variation in abundance among stops, we considered the simple occupancy model described by MacKenzie et al. (2002). Because this model implies the assumption of *constant abundance* across stops, we believe that it will frequently be untenable, although it may provide a reasonable approximation in some situations. However, because it is the only rigorous competitor that is capable of yielding biologically relevant information (i.e., patch occupancy) from sample data, we believe that many investigators would consider its use for some problems. We will label this model ''Model 0'' (M0).

We used AIC (Akaike 1973, Burnham and Anderson 1998) to compare the various models. Because the sample size in the present problem is the number of spatial samples (i.e., there are $R = 50$ $w_{i.}$'s in Eq. 5), we used the small-sample adjustment AIC_c (e.g., Burnham and Anderson 1998:221). In general, models with lower AIC_c scores are considered to be better candidate models than those with higher scores. In some analyses, one could make an argument for the use of an AIC statistic that adjusts for overdispersion. Instead, we choose to defer this issue of possible overdispersion to the next section (negative binomial). Our approach then deals explicitly with overdispersion by attempting to *model* it, rather than *adjusting* for it, and hence we do not consider other refinements to AIC beyond the small-sample correction.

For the various models fit to each species, we computed the MLEs of λ (for Models 1–3, as it is not available for Model 0), the various detection probability parameters, and the occupancy rate. In addition, for Models 1–3 the conditional detection probability, $\bar{p}_c$, was computed according to the discussion of section *Conditional and unconditional detection probability*, as this is the quantity comparable to the detection probability of MacKenzie et al. (2002). Because Models 2 and 3 contain a nonconstant detection probability, the value at the mean sample day was used (i.e., evaluating (11) at day $= \overline{\text{day}}$). The results for the five species are shown in Table 1. For each species, model results are ordered by AIC_c value, from best to worst, and AIC_c differences (Δ_m) and Akaike weights (w_m), where m is the model index (Burnham and Anderson 1998:122–124) are given to facilitate interpretation.

We see from Table 1 that one or more of the models that allow for variation in abundance (Models 1–3) are preferred to Model 0 in all cases. The Akaike weights for Model 0 are near zero in all cases except for the Gray Catbird, which is the only instance in which Model 0 beats any of the variable abundance models. For the Gray Catbird, $w_0 = 0.158$, which is still only one-fourth that of Model 1, for which $w_1 = 0.572$. In general, one might use the Akaike weights to carry-out ''model-averaging'' in order to obtain estimates of critical parameters averaged across the model set (Burnham and Anderson 1998), but in the case of Model 0, no abundance estimate is obtained. Moreover, even for occupancy, justification for averaging Model 0 results (which assumes constant abundance) with other models is unclear. Mean abundance estimates ($\hat{\lambda}$) are given in Table 1. To better gauge the uncertainty associated with these estimates, we computed 95% profile likelihood intervals for λ of each species using the model with the best AIC_c. Profile likelihood intervals are probably more suitable for this problem because of the low sample sizes where conventional asymptotic (Wald-type) intervals will tend to understate the confidence interval width. The 95% profile intervals for the five species are: Hermit Thrush (0.332, 2.098), Wood Thrush (1.624, 3.036), Gray Catbird (0.332, 0.941), Ovenbird (1.612, 2.779), and American Redstart (1.381, 3.869).

Generally, the conditional detection probability estimates (i.e., $\bar{p}_c$) are fairly similar across the various models, the main discrepancy being associated with Model 0 (as expected). Consequently, the estimates of occupancy for Model 0 depart from those estimates based on the variable abundance models, although the

TABLE 1. Results fitting Poisson abundance model to 50 spatial point counts of five bird species repeated 11 times. Model results for each species are ranked by AIC_c (w_i = Akaike weight), best to worst.

Model	λ	ψ	β_0	β_1	β_2	r	$\bar{p}_c$	AIC_c	Δ_i	w_i
Hermit Thrush										
M2	0.664	0.485	−2.545	−0.057		0.073	0.097	193.58	0	0.440
M1	0.678	0.492	−2.593			0.070	0.094	193.84	0.25	0.387
M3	0.652	0.479	−2.585	−0.058	0.0008	0.070	0.093	195.92	2.34	0.137
M0		0.417					0.109	198.59	5.00	0.036
Wood Thrush										
M1	2.208	0.890	−1.211			0.230	0.447	634.21	0	0.608
M2	2.221	0.891	−1.209	−0.004		0.223	0.448	636.39	2.19	0.204
M3	2.099	0.877	−0.972	0.008	−0.0023	0.275	0.499	636.55	2.34	0.188
M0		0.902					0.415	708.76	74.56	0.000
Gray Catbird										
M1	0.546	0.421	−1.520			0.179	0.222	298.38	0	0.572
M2	0.539	0.417	−1.528	0.009		0.178	0.220	300.44	2.07	0.204
M0		0.403					0.230	300.96	2.58	0.158
M3	0.536	0.415	−1.457	0.014	−0.0009	0.189	0.232	302.68	4.30	0.067
Ovenbird										
M1	2.238	0.893	−0.777			0.315	0.566	588.29	0	0.534
M2	2.265	0.896	−0.759	−0.014		0.319	0.574	589.13	0.85	0.350
M3	2.248	0.894	−0.709	−0.011	−0.0005	0.330	0.585	591.34	3.05	0.116
M0		0.860					0.533	698.41	110.12	0.000
American Redstart										
M1	2.169	0.886	−1.933			0.126	0.271	580.09	0	0.671
M2	2.196	0.888	−1.959	0.005		0.124	0.267	582.23	2.15	0.229
M3	2.138	0.882	−2.052	−0.004	0.0016	0.114	0.245	583.92	3.83	0.099
M0		0.842					0.283	592.90	12.81	0.001

Note: For a description of the models and symbols, see sections *Modeling Heterogeneity in p with Finite Mixtures* and *Application to Avian Point Counts.*

difference is not always large (e.g., for the Wood Thrush, the difference is on the order of 2–3%). The difference is most pronounced for the Hermit Thrush and American Redstart.

There is evidence of temporal variation in detection probability for the Hermit Thrush, in which case the linear change model (M2) is slightly preferred to the constant model (M1), but the Akaike weights are similar. The direction of temporal change (decrease in detection probability over time) is consistent with the expected reduction in detection probability as the breeding season progresses. Estimates of abundance (the Poisson mean) do not appear to be sensitive to the choice of model for detection probability.

An important benefit of Models 1–3 is that they allow for estimation of abundance, and these estimates appear reasonable, as do the estimates of animal-specific detection probabilities (i.e., r) , based on our informal assessment and knowledge of bird biology and sampling. In particular, the Ovenbird is typically easy to detect because of its distinctive call, and its estimated detection probability is $\hat{r} = 0.315$ (for Model 1), the highest among the five species. Similarly, our informal assessment is that the Ovenbird, Gray Catbird, and Wood Thrush are all easier to detect than both the American Redstart and Hermit Thrush, the latter having very low estimated detection probabilities. In general, detection probabilities will depend on the specific observer and other sampling protocol issues (which are controlled for in this study by use of the same observer and the same protocol in each sample); thus, detection probabilities for other surveys may very well differ from those obtained here.

Negative binomial results

We investigated the negative binomial model on abundance for these data. In all cases, maximum likelihood estimation appeared unstable, indicated by high correlation between the parameter estimates (typically between $\hat{r}$, the detection probability, and $\hat{\mu}$, the negative binomial mean) and flat likelihood surfaces. For example the correlation between $\hat{\mu}$ and $\hat{r}$ for the American Redstart was −0.998 and similar negative values between these two parameter estimates were found for the remaining four species. We attempted to compute 95% profile likelihood intervals for μ (the parameter of interest), and these intervals typically had an upper bound of ∞ (i.e., no finite value of μ could be found to yield a log-likelihood difference of 3.84). The single exception was for the Wood Thrush data, for which the 95% profile likelihood on μ was (5.79, 102.81). This highlights the main problem that we found in attempting to interpret the negative binomial results: the estimates, in most cases, were simply not sensible. For example, for the Wood Thrush, $\hat{\mu} = 29.7$ would suggest that the *average* point count is observing 29.7 Wood

Thrushes, which is certainly beyond the realm of possibility for point counts of most breeding song birds. The lone exception for which sensible negative binomial estimates were obtained was the Gray Catbird, for which $\hat{\mu} = 0.69$ (compared to $\hat{\lambda} = 0.56$ under the Poisson model). Even in this instance, the likelihood was extremely flat, yielding no finite upper bound on the profile likelihood.

Because of this apparent instability, we omit additional detail on the negative binomial results for these species, and we are cautious about considering this model as a viable candidate model for explaining detection–nondetection data from this BBS field experiment until this suspect behavior is better understood (see *Discussion*).

Simulation Study

Although the previous example offers some indication that the Poisson model provides sensible answers for real data, it remains to establish suitable frequentist properties of the estimators, i.e., their average behavior over a large number of data sets. As with any likelihood-based technique, we expect performance to deteriorate in small samples. We conducted a simulation study to evaluate estimation of the critical parameters in these occupancy problems under the Poisson model for abundance, and to assess what constitutes ''small'' sample sizes over a range of conditions. We also carried out a more limited simulation study to evaluate the performance of the MLE when the data-generating model is negative binomial.

See Appendix A for additional information on the simulation design. Results are given in Appendix B. We provide a summary of the salient points from that study here.

Discussion of simulation results

Poisson data-generating model.—Bias of $\hat{\lambda}$ is generally small over the range of situations considered in the simulations. Naturally, the largest bias occurs for low values of animal-specific capture probability (e.g., $r = 0.1$) and when fewer sites are sampled. In such cases, the bias is typically ~10–15%. This is not surprising, because when λ is small, the expected number of sites at which detection occurs also is small.

For this reason, it is difficult to extend simulation studies to smaller sample situations because, for example, with $R = 100$ sites, and over a broad range values of r and λ, one does not expect to collect much data. As an illustration, suppose that abundance does behave as a Poisson random variable with $\lambda = 0.5$. Then, occupancy rate is slightly less than 40%. We expect to see animals at *fewer* than 40 sites, depending on r and T. If $r = 0.1$ and $T = 5$, the expected number of sites at which animals are detected at all is only about 18 or 19. Expectations must be moderated in such situations, and one probably would not design a study with $T = 5$ and $R = 100$ if similar values of λ and r were suspected. We emphasize that likelihood-based inference is not a small-sample procedure, and this should be considered in *any* study. Thus, although it is tempting to consider R in the context of traditional capture–recapture, this is misleading because $R = 100$ does not generate 100 capture histories of animals detected at least once, but instead includes sites with all-zero capture histories.

Nevertheless, $\hat{\lambda}$ can perform very well for $R = 100$ or even less, under the right circumstances. For example, larger values of r and T provide more favorable conditions for estimating λ. Simulation results not presented here indicated that $T = 10$ may yield practical estimates for small values of r. Similarly, if r is larger, say ≥ 0.3, performance of the MLE of λ is adequate even for $T = 5$.

As a final comment on estimation of λ, we note that the distribution of $\hat{\lambda}$ is slightly skewed over the range of situations considered. Thus, although the bias of $\hat{\lambda}$ is apparent in the mean of the sampling distribution, the median is frequently very close to the truth over all situations considered, which may be some consolation for the observed small-sample bias.

Estimation of ψ.—In traditional capture–recapture problems for which estimation of abundance is the objective, failure to account for heterogeneity causes a negative bias in the estimator of N (e.g., see Seber 1982, Pollock et al. 1990). Thus, in occupancy surveys, we expect that failure to model heterogeneity will lead to negative bias in the occupancy rate estimator. We see this behavior clearly in the results given in Appendix B, where, regardless of the situation, the mean of $\hat{\psi}$ under the constant-p model described by MacKenzie et al. (2002) exhibits a negative bias. Conversely, there is almost no discernible bias in the estimator of ψ under the data-generating Poisson heterogeneity model when $R = 500$, and only slight bias in most cases when $R = 200$. As before, there is some skew in the distribution of $\hat{\psi}$. Also consistent with the results for $\hat{\lambda}$, the performance of $\hat{\psi}$ deteriorates somewhat as λ decreases, because this generally leads to fewer detection histories upon which to base inference.

Negative binomial data-generating model.—The sampling distribution of $\hat{\mu}$ under the negative binomial model is highly skewed. Consequently, the estimator of μ is considerably biased in the small-sample situation considered. We note that additional simulation results (not reported) indicate that this bias diminishes rapidly as either R or T is increased. To elucidate the results, we report medians (Table 3 of Appendix B) for summaries of estimators under the negative binomial data-generating model. In general, the sampling distributions of $\hat{\mu}$ and $\hat{\psi}$ are centered approximately on the truth, with (interestingly) slightly more discrepancy in the low-heterogeneity cases. As expected, when the Poisson model is fit to negative binomial data, we generally observe larger (negative) bias in the estimators of both the mean and occupancy rate, although the bias is minimal for the low-heterogeneity case, but quite substantial when there is extreme heterogeneity. The sampling distribution of $\hat{\lambda}$ is nearly normal, so the means are similar to the medians reported in Table 3 of Appendix B. Note that, although the bias in the estimation of the mean abundance may be substantial, occupancy rate estimates are less affected. Finally, the estimator of ψ using the constant-p model of MacKenzie et al. (2002) exhibits more bias than under the misspecified Poisson model, as expected.

Conclusions and Discussion

In this paper, we have developed a method for accounting for heterogeneous detection probabilities in replicated presence–absence data (i.e., ''occupancy surveys'') where the heterogeneity arises as a result of variation in abundance among sites. Although heterogeneity could be accounted for indirectly, in traditional methods, by inclusion of covariates in a model for p, it is not always possible to observe covariates that are correlated with abundance. The benefit of our approach is that it is based on the direct linkage between p_i and local abundance, N_i, which is a consequence of binomial sampling (i.e., Eq. 1). One important benefit of exploiting this linkage is that our approach allows for the estimation of the distribution of site-specific abundances, and even site-specific abundance. This is made possible by recognizing that variation in N induces heterogeneity in detection probabilities among sites. Therefore, the probability distribution of abundance can be deduced from the latent detection probability distribution.

As suggested in the *Introduction*, we believe that occupancy surveys have the potential to be useful in various kinds of ecological investigations. Because of the reduced effort typically associated with the collection of presence–absence data, we believe that occupancy surveys may prove very useful in large-scale surveys of various organisms. For example, some amphibian surveys involve repeat visits by investigators to wetlands, with sampling carried out at each visit in an attempt to ascertain presence of one or more species of interest. Such sampling should be much less intensive than the multiple-observer (Cook and Jacobson 1979) or capture–recapture (Wood et al. 1998) sampling usually required to obtain reasonable abundance estimates. Avian point counts can be used to draw inferences about abundance when distances to detected birds are recorded (Buckland et al. 2001), when multiple observers conduct the counts (Nichols et al. 2000), or when the timing of detections is recorded (Farnsworth et al. 2002). However, for standard point counts that do not include collection of such ancillary data, when distance measurements are imprecise, or when there is ambiguity in the number of unique birds seen, inference about abundance is not really possible without very restrictive assumptions about stationarity of detection probabilities (e.g., see Nichols et al. 2000, Anderson 2001, Rosenstock et al. 2002). However, repeat point counts at sample locations with associated records of presence–absence could be used with occupancy models in order to provide reasonable inferences about the proportion of the area occupied by species. In these examples of avian and amphibian surveys, presence–absence will be ascertained by visual or auditory detection of animals. In the case of some secretive species of mammals, it may be reasonable to conduct occupancy surveys using automated remote detections (e.g., camera-trapping) or detections of animal sign (scats, tracks). For example, sign-based surveys of tiger occupancy of sample units will be much less expensive in time and effort than methods of abundance estimation based on detections of marked animals (Karanth and Nichols 2002). The approach described in this paper uses the data from occupancy surveys to draw inferences not only about proportional occupancy of sample units, but also about abundance in some situations.

We believe that such occupancy surveys also will be useful in metapopulation studies involving multiple visits to many different sites among which animal movement is hypothesized. As noted in the *Introduction*, the proportion of patches occupied is the state variable of interest in many metapopulation models (e.g., Levins 1969, 1970, Lande 1987, 1988, Hanski 1992, 1994, 1997). In association with metapopulation studies, substantial effort has been directed at parameterizing so-called ''incidence functions'' (Diamond 1975, Hanski 1992) characterizing the probability of occurrence as a function of patch characteristics. The methods presented here provide a means of properly estimating occupancy probabilities and associated functional relationships when there is heterogeneity of detection probabilities associated with variation in abundances over patches or sampling units.

In addition to reasonable estimation of occupancy rates, the information on the distribution of abundances over sampling units may be very useful in metapopulation studies as well. Metapopulation models range from very simple to fairly complex. Under the simplest models (e.g., Levins 1969, 1970), all patches are assumed to be equal with respect to the parameters governing patch occupancy dynamics, local colonization, and extinction probabilities. Perhaps the most detailed metapopulation models involve the use of structured multisite matrix models that model the abundance of each age or stage class at each location as functions of class- and location-specific vital rates and rates of movement (e.g., see Rogers 1966, Le Bras 1971, Schoen 1988, Lebreton 1996, Lebreton et al. 2000). Models of intermediate complexity and detail include those of Gyllenberg and Hanski (1992) and Gyllenberg et al. (1997), in which the abundance or population size of each patch is a state variable of interest. This is a very reasonable state variable, because extinction probability depends very strongly on abundance (e.g., Bailey 1964, MacArthur and Wilson 1967, Goel and Richter-Dyn 1974, Gilpin and Soulé 1986, Boyce 1992), and dispersal and vital rates are frequently modeled as functions of abundance (density dependence) as well. The distribution of abundance over patches is one of the summary statistics used to characterize metapopulation systems under the models of Gyllenberg and Hanski (1992) and Gyllenberg et al. (1997), which indeed predict an equilibrium abundance distribution. The methods presented in this paper provide a means of estimating this distribution and thus yield opportunities to test model predictions.

It is often the case that little additional information beyond simple presence–absence is available. In such cases, reduction of data to presence–absence may be appropriate or may entail little loss of information. For example, even when counts of organisms are made (such as in avian point counts), it may not be possible to determine the number of *unique* individuals that were observed due to movement of individuals or imprecise locational information. A second example, mentioned previously, is that of anuran surveys, in which it is often very difficult to generate a useful ordinal measure of abundance beyond simple presence or absence. Thirdly, in carnivore scent station surveys, it is not always possible to determine the number of unique individuals that have visited a particular scent station. Finally, in the monitoring of rare organisms, or those that are difficult to detect, the detection of multiple organisms may seldom occur. Consequently, even in problems where additional information may be available in the form of counts or similar statistics, it is often not clear how such information can be brought to bear in a rigorous manner toward assessing questions having to do with occupancy. This is not to say that we recommend collecting only presence–absence data where it is possible to collect other types of information. In fact, we strongly discourage such methods, as techniques may evolve that allow for such information to be used. However, at this time no general methods exist for dealing with every type of data that biologists might collect regarding abundance. Our method provides abundance estimates from presence–absence data that may be collected directly or obtained by reduction of other information to presence–absence data.

Alternative latent abundance models.—In our development and analyses, we have considered models for the latent distribution of p_i based on parametric forms implied by Poisson and negative binomial distributions on abundance. Thus, the latent p_i distribution has support on the integers $1 - (1 - r)^k$; $k = 0, 1, 2, \ldots$, with probabilities f_k proportional to the Poisson (or negative binomial) density. The benefit of this approach is that there are only two (or three) parameters to be estimated, and the number of parameters does not increase with the number of support points considered, in contrast to the ''nonparametric'' approach of Norris and Pollock (1996). In addition, the parametric approach seems to be the most logical modeling approach for this problem because the distribution structure of p_i is entirely a consequence of that on site-specific abundance. Nevertheless, one could adopt a nonparametric approach, choosing to estimate both the support points and their masses with no imposed ''ultrastructural'' relationships, consistent with the approach of Norris and Pollock (1996). However, in doing so, the number of support points that can be considered is severely limited by the number of sampling occasions. Such nonparametric estimation can lead to bias in the parameter estimates, and hence abundance estimation, depending on the coarseness of the finite approximation to the true distribution of N. Nevertheless, this approach may be preferred when assumption of parametric forms is not desirable. It is not clear, however, whether or not sufficiently complex nonparametric finite mixtures may be estimated from simple presence–absence data.

We have given only brief consideration to the negative binomial model for N, which allows overdispersion relative to the Poisson assumption. Simulation results are encouraging, and suggest that the model parameters may be reasonably well estimated. However, our attempts to fit this model to avian point-count data were not satisfactory, resulting in flat likelihoods, highly correlated parameter estimates, and estimates that are at odds with our understanding of the problem. In short, the negative binomial parameters appear to be poorly identified by the BBS data considered. This is not necessarily an indictment of the negative binomial model, and may simply be due to small sample size estimation under that complex model, or additional pathologies in the data not considered here.

Where possible, we feel that extra-Poisson variation in site-specific abundance is best modeled with the aid of sensible explanatory covariates. The modeling framework presented here extends trivially to this situation, simply by specification of the log-linear model on site-specific means, λ_i:

$$\log(\lambda_i) = \sum_{j=1}^{p} x_{ij}\beta_j.$$

For amphibian or waterfowl surveys on wetland basins, an important covariate might be the area of the wetland being sampled. With sufficient additional information (x_j's), we think that most substantial overdispersion due to variation in abundance can be accounted for explicitly in this manner. One reviewer also suggested the use of quasi-likelihood to model overdispersion in abundance, which may be a viable approach. Additional analysis of the negative binomial and other approaches to modeling variation in detection due to variable abundance require further study.

Our main reason for focusing on the Poisson model is its motivation as arising under a random distribution of individuals in space. Clearly, the negative binomial is an important generalization of this, allowing for (spatial) variation in mean abundance. Although the negative binomial is appealing for this reason, we question whether overdispersed models (relative to the Poisson assumption) are sensible in many contexts. For example, breeding birds, because they are territorial, are probably more likely to be distributed in space in a manner that suggests *under*-dispersion relative to the Poisson model. Research in this regard is also needed.

Design considerations.—Successful application of our approach depends critically on the ability to characterize the variability in detection probabilities. There are many factors that affect this ability. One of the more important factors in this regard is the number of sampling sites. As with traditional applications of complex capture–recapture models allowing for heterogeneity among individuals, good performance of the estimators requires large sample sizes (i.e., many observed capture histories). This is often neglected in applications of capture–recapture methods because one cannot design a study to observe a desired number of individuals.

Our simulation studies indicate little bias in the estimators of both mean abundance and occupancy rate under a range of conditions. We feel that our simulation studies encompass a broad range of practical sampling scenarios for monitoring programs and large-scale field investigations. We did not extensively investigate small-sample extremes because estimator performance under these situations is highly variable. In short, when heterogeneity exists as a result of variation in abundance, several hundred sample sites may be necessary to provide reasonable estimates of mean abundance and occupancy rate, although it may be possible to realize success with many fewer. Precise guidance is very sensitive to context. In general, because the essence of any occupancy study is a binomial sampling model (occupied or not), sample sizes should be considered within this context.

The number of sampling occasions is also an important consideration. For the range of situations that we considered, $T = 5$ may be adequate for many intents and purposes, but larger T can be advantageous when it is practical to achieve while still satisfying the closure assumption. Although abundance is not usually a controllable factor (unlike T and R), the mean site-specific abundance has important consequences for the performance of maximum likelihood estimators. If N is large, on average, then animals will be detected almost all of the time and no variability among the p_i's will be observed (unless r is very small). Thus, there will be little ability to characterize the distribution of abundances. Although this leads to an ''apparent constant-p'' situation for which the MacKenzie et al. (2002) method would be well suited, it also would suggest very high occupancy rates under the Poisson model. In such cases, one might consider alternative mixing distributions on abundance that allow more flexibility in occupancy rate, perhaps nonparametric finite mixtures. Alternatively, in problems where the size of the sample unit size can be controlled to some extent, this may allow some flexibility in the control of mean abundance. That is, mean abundance is scale specific, and the choice of sample unit determines the scale at which model parameters are defined. Conversely, very low ''mean abundance'' yields either $N = 1$ or $N = 0$, and this case is essentially that considered by MacKenzie et al. (2002). These considerations lead to the recommendation to evaluate different designs using simulations tailored to anticipated sampling conditions.

Extensions.—The proposed method applies to repeated point counts that may be reduced to detection–nondetection data. In general, however, there is some loss of information in reduction to binary data. For example, if one observes $y_{it} = 2$, then it is known that N_i must be ≥ 2. This can be accounted for by generalizing the observation model to a product binomial likelihood. When mean abundance is low, which will tend to happen whenever the sampling unit is small in relation to animal density, we suspect that there will be little difference between the two approaches. Other types of sampling schemes, including common anuran monitoring programs, give rise to multinomial categories of abundance (e.g., none, few, many). The possibility exists for extracting abundance information from these data also, but the form of the likelihood (as it relates to abundance) is less clear in this instance. We are currently investigating these extensions in the context of several monitoring programs involving point counts of birds and waterfowl.

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Literature Cited

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267–281 *in* B. N. Petrov and F. Csaki, editors. Second International Symposium on Information Theory. Akademiai Kiado, Budapest, Hungary.

Anderson, D. R. 2001. The need to get the basics right in wildlife field studies. Wildlife Society Bulletin **29**:1294–1297.

Azuma, D. L., J. A. Baldwin, and B. R. Noon. 1990. Estimating the occupancy of Spotted Owl habitat areas by sampling and adjusting bias. USDA Forest Service General Technical Report **PSW-124**.

Bailey, N. T. J. 1964. The elements of stochastic processes with applications to the natural sciences. John Wiley, New York, New York, USA.

Bayley, P. B., and J. T. Peterson. 2001. An approach to estimate probability of presence and richness of fish species. Transactions of the American Fisheries Society **130**:620–633.

Boyce, M. S. 1992. Population viability analysis. Annual Review of Ecology and Systematics **23**:481–506.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling. Oxford University Press, Oxford, UK.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Burnham, K. P., and W. S. Overton. 1978. Estimation of the size of a closed population when capture probabilities vary among animals. Biometrika **65**:625–633.

Cochran, W. G. 1977. Sampling techniques. Third edition. John Wiley, New York, New York, USA.

Cook, R. D., and J. O. Jacobson. 1979. A design for estimating visibility bias in aerial surveys. Biometrics **35**:735–742.

Diamond, J. M. 1975. Assembly of species communities. Pages 342–444 *in* M. L. Cody and J. M. Diamond, editors. Ecology and evolution of communities. Harvard University Press, Cambridge, Massachusetts, USA.

Dorazio, R. M., and J. A. Royle. 2002. Estimation of population size using a beta-binomial mixture to model heterogeneous rates of capture or detection. Biometrics.

Farnsworth, G. L., K. H. Pollock, J. D. Nichols, T. R. Simons, J. E. Hines, and J. R. Sauer. 2002. A removal model for estimating detection probabilities from point count surveys. Auk **119**:414–425.

Geissler, P. H., and M. R. Fuller. 1987. Estimation of the proportion of area occupied by an animal species. Proceedings of the Section on Survey Research Methods of the American Statistical Association **1986**:533–538.

Gilpin, M. E., and M. E. Soulé. 1986. Minimum viable populations: processes of species extinctions. Pages 19–34 *in* M. E. Soulé, editor. Conservation biology: the science of scarcity and diversity. Sinauer, Sunderland, Massachusetts, USA.

Goel, N. S., and N. Richter-Dyn. 1974. Stochastic models in biology. Academic Press, New York, New York, USA.

Gyllenberg, M., and I. Hanski. 1992. Single species metapopulation dynamics: a structured model. Theoretical Population Biology **42**:35–61.

Gyllenberg, M., I. Hanski, and A. Hastings. 1997. Structured metapopulation models. Pages 93–122 *in* I. A. Hanski and M. E. Gilpin, editors. Metapopulation biology. Academic Press, San Diego, California, USA.

Hall, D. B. 2000. Zero-inflated Poisson and Binomial regression with random effects: a case study. Biometrics **56**: 1030–1039.

Hanski, I. 1992. Inferences from ecological incidence functions. American Naturalist **139**:657–662.

Hanski, I. 1994. A practical model of metapopulation dynamics. Journal of Animal Ecology **63**:151–162.

Hanski, I. 1997. Metapopulation dynamics: from concepts and observations to predictive models. Pages 69–91 *in* I. A. Hanski and M. E. Gilpin, editors. Metapopulation biology: ecology, genetics, and evolution. Academic Press, New York, New York, USA.

Hanski, I. A., and M. E. Gilpin, editors. 1997. Metapopulation biology: ecology, genetics, and evolution. Academic Press, San Diego, California, USA.

Karanth, K. U., and J. D. Nichols, editors. 2002. Monitoring tigers and their prey. Centre for Wildlife Studies, Bangalore, India.

Lancia, R. A., J. D. Nichols, and K. H. Pollock. 1994. Estimating the number of animals in wildlife populations. Pages 215–253 *in* T. Bookhout, editor. Research and management techniques for wildlife and habitats. The Wildlife Society, Bethesda, Maryland, USA.

Lande, R. 1987. Extinction thresholds in demographic models of territorial populations. American Naturalist **130**:624–635.

Lande, R. 1988. Demographic models of the Northern Spotted Owl (*Strix occidentalis caurina*). Oecologia **75**:601–607.

Lawless, J. F. 1987. Negative binomial and mixed Poisson regression. Canadian Journal of Statistics **15**:209–225.

LeBras, H. 1971. Equilibre et croissance des populations soumises a des migrations. Theoretical Population Biology **2**:100–121.

Lebreton, J.-D. 1996. Demographic models for subdivided populations: the renewal equation approach. Theoretical Population Biology **49**:291–313.

Lebreton, J.-D., M. Khaladi, and V. Grosbois. 2000. An explicit approach to evolutionary stable dispersal strategies: no cost of dispersal. Mathematical Biosciences **165**:163–176.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America **15**:237–240.

Levins, R. 1970. Extinction. Pages 77–107 *in* M. Gerstenhaber, editor. Some mathematical questions in biology. Volume II. American Mathematical Society, Providence, Rhode Island, USA.

Link, W. A., R. J. Barker, J. R. Sauer, and S. Droege. 1994. Within-site variability in surveys of wildlife populations. Ecology **74**:1097–1108.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey, USA.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology **83**:2248–2255.

Nichols, J. D., J. E. Hines, J. R. Sauer, F. W. Fallon, J. E. Fallon, and P. J. Heglund. 2000. A double-observer approach for estimating detection probability and abundance from point counts. Auk **117**:393–408.

Nichols, J. D., and K. U. Karanth. 2002. Statistical concepts; assessing spatial distribution. *In* K. U. Karanth and J. D. Nichols, editors. Monitoring tigers and their prey. Centre for Wildlife Studies, Bangalore, India. *In press.*

Norris, J. L. III, and K. H. Pollock. 1996. Nonparametric MLE under two closed capture–recapture models with heterogeneity. Biometrics **52**:639–649.

Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. Wildlife Monographs **62**:1–135.

Pledger, S. 2000. Unified maximum likelihood estimates for closed capture-recapture models using mixtures. Biometrics **56**:434–442.

Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture–recapture experiments. Wildlife Monographs 107.

Robbins, C. S., D. A. Bystrak, and P. H. Geissler. 1986. The Breeding Bird Survey: its first fifteen years, 1965–1979. U.S. Department of Interior, Fish and Wildlife Service Resource Publication 157, Washington, D.C., USA.

Rogers, A. 1966. The multiregional matrix growth operator and the stable interregional age structure. Demography **3**: 537–544.

Rosenstock, S. S., D. R. Anderson, K. M. Giesen, T. Luekering, and M. F. Carter. 2002. Landbird counting techniques: current practices and an alternative. Auk **119**:46–53.

Schoen, R. 1988. Modeling multigroup populations. Plenum Press, New York, New York, USA.

Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. Second edition. Charles Griffin, London, UK.

Skalski, J. R. 1994. Estimating wildlife populations based on incomplete area surveys. Wildlife Society Bulletin **22**: 192–203.

Thompson, S. K. 1992. Sampling. John Wiley, New York, New York, USA.

Thompson, W. L., G. C. White, and C. Gowan. 1998. Monitoring vertebrate populations. Academic Press, San Diego, California, USA.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations. Academic Press, San Diego, California, USA.

Wood, K. V., J. D. Nichols, H. F. Percival, and J. E. Hines. 1998. Size–sex variation in survival rates and abundance of pig frogs, *Rana grylio*, in northern Florida wetlands. Journal of Herpetology **32**:527–535.

Yoccoz, N. G., J. D. Nichols, and T. Boulinier. 2001. Monitoring of biological diversity in space and time; concepts, methods and designs. Trends in Ecology and Evolution **16**: 446–453.

APPENDIX A

A description of the simulation design is available in ESA's Electronic Data Archive: *Ecological Archives* E084-015-A1.

APPENDIX B

Tables presenting simulation results are available in ESA's Electronic Data Archive: *Ecological Archives* E084-015-A2.